动 物 学 研 究 2006, Jun. 27(3): 225－234 CN 53－1040/Q ISSN 0254－5853
Zoological Research

Distribution and Ecology of the Western Ecuador Frog *Leptodactylus labrosus* (Amphibia: Anura: Leptodactylidae)

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Abstract: *Leptodactylus labrosus* is a terrestrial sit-and-wait predator; its diet includes ground-level, fossorial, and flying insects, and ants numerically predominate. *Bothrops asper* is recorded as a predator of *L. labrosus*. *L. labrosus* lives mainly in deciduous and semi-deciduous forests, where it is restricted to wet microhabitats, and occasionally in evergreen forests. *L. labrosus* inhabits northern, central, and southern regions of western coastal Ecuador and northern and central western coastal Peru up to 700 m, and into the dry interandean valleys of southern Ecuador and northern Peru up to 1 300 m. Its distribution encompasses moistly seasonally dry forest in coastal Ecuador and Peru. It also occupies moister areas towards the slopes of the Andes where it is sympatric with three other congeneric species, but at sites of sympatry the species show habitat segregation. The distribution pattern of *L. labrosus* is shared by several other range-restricted amphibians corresponding to the Tumbesian region, which should be recognized as an endemic Amphibian area. The zone between the Choco and Tumbesian regions, where *L. labrosus* gets in sympatry with other *Leptodactylus* species, possess ecological and climatic characteristics that have shaped a unique fauna, including several endemic taxa; and it should be recognized as the west Ecuadorian endemic region.

Key words: *Leptodactylus*; Distribution; Endemism area; Ecuador

厄瓜多尔西部新热带蛙(两栖纲:无尾目:细趾蟾科)的分布特征及生态习性

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摘要: *Leptodactylus labrosus* 属于陆地坐－等型的捕食者, 其食物包括地表的、掘地的及飞行昆虫, 其中蚂蚁数量最多。曾有报道 *Bothrops asper* 是其天敌。*L. labrosus* 主要栖息于落叶及半落叶林潮湿的环境中, 偶尔也栖息于常绿林中。*L. labrosus* 分布于厄瓜多尔西海岸的北部、中部、南部; 秘鲁西海岸的北部、中部, 分布地海拔可达 600 m; 及位于南厄瓜多尔和北秘鲁海拔高达 1 300 m 的干燥的安第斯山谷。其分布地区包括了厄瓜多尔和秘鲁海岸的潮湿的、季节性干燥的森林。在安第斯山脉斜坡的潮湿地带, *L. labrosus* 与其他 3 种细趾蟾科的分布区重叠, 但表现为生境分离。其分布特征与其他几种活动区域受限的两栖动物相似。Tumbesian 地区应被认为是地方特有两栖动物的分布区。Choco 和 Tumbesian 的中间区域是 *L. labrosus* 与其他细趾蟾科的生境分布重叠区, 其生态及气候特征使其形成了独特的动物区系, 包括几种地方特有物种。因此该地区应被划为西厄瓜多尔地方种区域。

关键词: 细趾蟾科; 分布; 地方种区域; 厄瓜多尔
中图分类号: Q959.53; Q958 **文献标识码:** A **文章编号:** 0254－5853(2006)03－0225－010

Received date: 2005－11－21; Accepted date: 2006－03－27
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收稿日期: 2005－11－21; 接受日期: 2006－03－27

Frogs of the genus *Leptodactylus* (Amphibia, Leptodactylidae) are moderately diversified in the Neotropics; 70 species are currently recognized (Frost, 2004; Heyer, 2005). Thirteen species of *Leptodactylus* are reported from Ecuador, and six occur in the west of the Andes: *Leptodactylus labrosus*, *L. melanonotus*, *L. peritoaktites*, *L. rhodomerus*, and *L. ventrimaculatus* (Coloma, 2005 – 2006; Frost, 2004; Heyer, 2005). Scant ecological information is known from the populations of *Leptodactylus* living in western Ecuador. *L. labrosus* has been mentioned few times in the literature since its description by Marcos Jiménez de la Espada in 1875, and most references dealt with its taxonomy and natural history.

The name *Leptodactylus labrosus* Jiménez de la Espad was associated with the species that inhabit in the xeric parts of southwestern Ecuator and northwestern Peru by Heyer & Peters (1971), who reported that *L. labrosus* occurs on the floor of scrub forest as well as in and about drainage ditches and bushes in local farms. Heyer (1978) characterized the species based on specimens from Ecuador and Peru, commenting on its sexual dimorphism (with females having longer femurs than males), and zoogeography in relationship with other species of the *L. fuscus* group. Heyer & Maxson (1982a) analyzed the biogeography of a morphological cluster formed by *L. labrosus/ventrimaculatus/bufonius/troglodytes*. *L. curtus* Barbour & Noble, 1920 was synonymized with *L. labrosus* by Heyer & Peters (1971). *L. labrosus* was located into the *L. fuscus* grouped by Heyer (1978), but Larson & de Sá (1998) found that based on chondrocranial characters *L. labrosus* is more related to species in the *L. pentadactylus* group.

The distribution of *L. labrosus* currently reported includes the dry coast from central western Ecuador to central western Peru, and the interandean valleys of Peru (Heyer & Peters, 1971; Heyer, 1978; Frost, 2004). Several specimens of *Leptodactylus* have been collected during recent expeditions at diverse localities in western Ecuador. In this paper, I describe the distribution pattern and general aspects of the ecology of *L. labrosus*, and provide some considerations on the biogeography and endemism areas of western Ecuador.

1 Materials and Methods

To analyze the habitat, microhabitat, activity, and diet of *L. labrosus*, I combine data from my own fieldwork and the material deposited at museums collected at various localities in western Ecuador (Tab. 1, Appendix 1). To analyze the distribution of *L. labrosus*, I referenced data from other published studies with confirmed distributional data (Tab. 1, Appendix 1). Eleven frogs, from four localities in southern Ecuador (Appendix 1) either collected by myself or recorded by the material from museum, were selected for diet analysis (selection criteria: euthanized within four hours after collection to prevent lost of data due to digestion).

Tab. 1 Ecuadorian localities mentioned in the text where the information for *L. labrosus* was recorded

Localities, provinces	Coordinates	Altitude (m)	Source
ECUADOR			
Agua Blanca, Machalilla National Park, Manabí	ca. 01°32′S, 80°44′W	150	1, 10
Arenillas, El Oro	03°33′S, 80°04′W	70	10
Buenaventura, El Oro	ca. 03°35′S, 79°53′W	600	3, 10
Cordillera Mangahurquillo, Loja	04°04′S, 80°18′W	325	2, 10
Cosanga, Valle, Loja	03°59′S, 79°21′W	1 500	3, 5, 8
Guayaquil and Cuatro Hermanitos, Guayas	02°10′S, 79°56′W	150	3, 5
La Troncal, Cañar	02°24′S, 79°20′W	460	10
Machala, El Oro	03°16′S, 79°58′W	35	3, 5, 10
Naranjal, Guayas	02°40′S, 79°36′W	30	10
Pimocha, Los Ríos	01°50′S, 79°36′W	33	3, 5, 6, 10
Playa Escondida, Esmeraldas	ca. 00°49′N, 80°00′W	0	10
Puyango, El Oro	03°52′S, 80°05′W	550	3
Quebrada de El Faique, Loja	04°10′S, 80°02′W	ca. 400	2, 10
Quevedo, Los Ríos	01°02′S, 79°27′W	ca. 100	3
Río Palenque Scientific/Biological Center	00°34′S, 79°20′W	220	3, 4, 7, 10
Same, Esmeraldas	ca. 00°50′N, 79°56′W	0	10
Tamarindo, Azuay	ca. 02°47′S, 79°33′W	400	10

Sources include: 1, Albuja & Muñoz, 1997; 2, Díaz & Baus, 2001; 3, Heyer, 1978; 4, Heyer & Maxson, 1982a; 5, Heyer & Peters, 1971; 6, Jimenez, 1875; 7, Larson & de Sá, 1998; 8, Parker, 1938; 9, Parker & Carr, 1992; 10, this study.

Stomachs were removed, opened, and then the contents were separated and spread in Petri dishes for identification. The prey were identified to family level when possible, counted and measured with a digital caliper for length and width (0.01 mm). Volume of individual prey items was calculated with the formula for a prolate spheroid: Volume = $4/3\pi(1/2 \text{ prey length}) \times (1/2 \text{ prey width})^2$. Means are presented as ± 1 *SE*. Relative prey mass value was calculated with the formula: prey mass/predator mass. The localities and their geographic coordinates and elevations were determined by researcher's field notes and museum records, and revised according to IGM (2000) (Tab. 1, Appendix 1). The classification of vegetation formations is taken from the proposal of Sierra (1999). The abbreviations used in the text include: Universidad San Francisco de Quito, Quito (DFCH-USFQ); División de Herpetología, Museo Ecuatoriano de Ciencias Naturales, Quito (MYM field-series and MECN); Fundación Herpetológica G. Orcés, Quito (FHGO); and Departamento de Biología, Escuela Politécnica Nacional, Quito (EPN).

2 Results

2.1 Ecological notes

L. labrosus (Fig. 1) was found in a variety of vegetation formations (Tab. 1, Appendix 1): Lowland Deciduous Forest (Agua Blanca and Machala), Lowland Semi-deciduous Forest (Playa Escondida), Foothill Semi-deciduous Forest (Cordillera Mangahurquillo, Quebrada de El Faique, and Puyango), and Foothill Evergreen Forest (Tamarindo). The individuals were in disturbed secondary forest (77%), forest borders, and open areas near forests (9%) or near buildings (14%). The frogs from deciduous and semi-deciduous habitats were primarily along the margins of or in streams (0.5 – 18 m width); while in evergreen habitats they were found as far as 100 m away from streams. Although several microhabitats were available at the various sites, the individuals of *L. labrosus* were mainly encountered on leaf litter, especially at stream margins. One individual was observed on a low bush 20 cm above ground, and another in water. *L. labrosus* is relatively uncommon everywhere, although it seems to reach higher densities in semi-deciduous forests than in deciduous or evergreen forest. *L. labrosus* occurred mainly during the evening, but a few individuals were seen also during late afternoon.

2.2 Preys

The diet of the studied *L. labrosus* includes 18 prey categories, all invertebrates. These categories can

Fig. 1 Adult *Leptodactylus labrosus* observed at night on a Bambu plantation, on the margin of a small stream, at the Centro Científico Río Palenque, province of Los Ríos, Ecuador, 11 November 2004

be grouped into adult insects, larval insects, spiders, gastropods, millipedes, and earthworms. Forty-nine prey items were identified: 80 % adult insects, 10 % larval insects, 4 % spiders, 2 % gastropods, 2 % millipedes, and 2 % earthworms. Mean number of preys per individual was 4.5 ± 2.8 preys (range 1.0 – 32.0 preys, $n = 12$). Mean length of prey items consumed was 9 ± 2.4 mm (range 1.1 – 120 mm, $n = 49$) with 78 % of prey between 3 – 17 mm length; mean width was 2.5 ± 0.3 mm (range 0.3 – 10.0 mm, $n = 49$) with 71 % of prey between 1.5 – 4 mm width, and mean volume was 189.7 ± 78.4 cm^3 (range = 0.04 – 1 570.8 mm, $n = 49$) with 75 % between 3.5 – 42.5 cm^3. There were no detectable relationships between mean prey volume per frog and frog SVL (snout to vent length) (log 10 transformed, $R = -0.41$, $P > 0.2$), mean prey length per frog and frog SVL (log 10 transformed, $R = -0.36$, $P > 0.2$), mean prey width per frog and frog SVL (log 10 transformed, $R = -0.31$, $P > 0.2$) or number of prey and frog SVL (log 10 transformed, $R = -0.16$, $P > 0.2$). However, due to small sample size, these results can not be considered conclusive.

The diet was dominated numerically (49%) by ants (Himenoptera, Formicidae) (Tab. 2). One frog (43.2 mm SVL) had eaten 21 ants, and 27% of frogs ate at least one ant. Adult coleopterans and orthopterans accounted for 16.3% of the prey and were also present in 27% of the individuals. Three of 18 prey categories were toxic arthropods (large spiders, millipedes, and spiny lepidopteran larvae), representing 8.2% of the diet (Tab. 2). One frog (44.0 mm SVL) ate a large spider and a large spiny lepidopteran larva (several spines had penetrated the stomach wall). Plant

Tab. 2 The summary of the diet of eleven specimens of *L. labrosus* from four localities in southwestern Ecuador

Category	Presa	No.	% No.	Vol. (cm^3)	% Vol.	Freq.
1	Annelida	1	2	1 570.8	31	1
2	Arachnida	2	4	301.6	6	2
	Coleoptera	5	10	130.4	3	3
3	Chrysomelidae	1	2	28.9	1	1
4	Cicindelidae larva	1	2	42.5	1	1
5	Elateridae	2	4	58.9	1	2
6	Scarabeidae	1	2	0.04	0.001	1
7	Diplopoda	1	2	6	0.1	1
8	Diptera	3	6	10.6	0.2	1
9	Gastropoda	1	2	890.1	18	1
	Hemiptera	2	4	20.9	0.4	1
10	Cicadellidae	2	4	20.9	0.4	1
	Himenoptera	24	49	208.0	4	3
11	Formicidae	24	49	208.0	4	3
	Lepidoptera	4	8	794.1	16	3
12	Fam. 1	2	4	0.4	0.01	2
13	Geometridae larva	1	2	8.3	0.2	1
14	Fam. 2 larva	1	2	785.4	16	1
	Neuroptera	2	4	35.6	0.7	2
15	Myrmeleontidae larvae	2	4	35.6	0.7	2
	Orthoptera	4	8	1 064.6	21	3
16	Grillotalpidae	1	2	1	0.02	1
17	Gryllidae	2	4	601.9	12	1
18	Tettigoniidae	1	2	461.8	9	1
	SUMS	49	100	5 033.7	100	–

Frequency (Freq) is the number of frogs in the sample containing a specific prey.

material was rare in the digestive tract, but stones and soil were abundant, especially in frogs that contained primarily fossorial prey in their stomach (mole crickets, antlions, and earthworms). Volumetrically, the diet of *L. labrosus* is dominated by earthworms (Annelida), crickets, grasshoppers and mole crickets (Orthoptera), slugs (Gastropoda), and caterpillars (Lepidoptera larvae) (Tab. 2). Individuals of Annelida, Gastropoda, Lepidoptera (larva), Tettigoniidae/Orthoptera, Gryllidae/Orthoptera, and Arachnida represented the highest prey volume in relation to frog SVL.

2.3 Predators

I analyzed the stomach content of a small *Bothrops asper* (FHGO 0535) collected in the surroundings of Machala, on 06 August 1992 by C. Solís, and found that the pitviper had eaten one *L. labrosus* (DFCH-USFQ 705). Measurements for the frog were 52.2 mm SVL, 15.7 mm head width, 17.8 mm head length, and 26.5 mm tibia length; mass (preserved and drained) was 9.8 g. The predator, a juvenile male *B. asper*, measured 322 mm SVL, 47 mm tail length, 16 mm head length, 12 mm head width and weighed (preserved and drained) 8.9 g. The frog, ingested legs first, was almost intact except for some digestion at the head and ventral skin. Relative prey mass is 1.1. *Porthidium arcosae* is sympatric with *B. asper* and *L. labrosus* in the Machalilla National Park and along the northern part of the province of Manabí. This hognosed pitviper is a potential predator of *L. labrosus*, as its juveniles eat frogs in captivity (pers. obs.). Other potential snake predators known to be sympatric with *L. labrosus* are *Chironius monticola*, *C. grandisquamis*, *Drymarchon melanurus*, *Dryadophis* (*Mastigodryas*) cf. *melanolomus*, *D. pulchriceps*, and *Leptodeira septentrionalis*.

2.4 Distribution

In Ecuador, *L. labrosus* is distributed in northern, central, and southern regions of western coastal Ecuador up to 600 m a.s.l. (highest record in the coastal region at Buenaventura); and into the dry inter-Andean valleys of southern Ecuador up to 1 300 m a.s.l. (highest record in inter-Andean valleys at the province of Loja) (Fig. 2). The most northern localities for the entire range of *L. labrosus* are Playa Escondida and Same, province of Esmeraldas, Ecuador. In northern Ecuador (from 0° up to Colombian border),

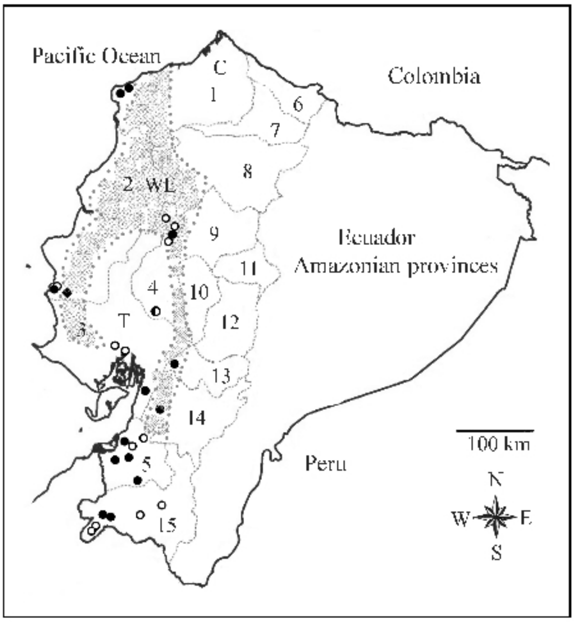

Fig. 2　The distribution of *L. labrosus* (circles) in Ecuador

Close symbols represent localities of examined material; open symbols represent literature record; half-close symbol represents type locality. Diamond represents the isolated population of *L. ventrimaculatus*. Shaded area between thick-dotted lines corresponds to the west Ecuadorian endemic region (WE). C = Chocó region, T = Tumbesian region. Numbers corresponds to mainland Ecuadorian provinces: 1, Esmeraldas; 2, Manabí; 3, Guayas; 4, Los Ríos; 5, El Oro; 6, Carchi; 7, Imbabura; 8, Pichincha; 9, Cotopaxi; 10, Bolivar; 11, Tungurahua; 12, Chimborazo; 13, Cañar; 14, Azuay; 15, Loja. The borders of the Amazonian provinces of Ecuador are not included for clearness of the figure. Continuous thick line: international border; thin dotted line: borders of provinces.

L. labrosus inhabits a narrow belt of Lowland Semi-deciduous Forest that extends along the coast of the province of Esmeraldas; in the central region (between 0° and 3°), it inhabits Lowland Deciduous Forests, and Seasonal Lowland Evergreen Forests; and in the southern region (from 3° south to Peruvian border), Lowland Deciduous Forests, Foothill Semi-deciduous Forests, and Foothill Evergreen Forests.

Eleven localities for *L. labrosus* are here analyzed (Appendix 1), which confirm that it is the only species of the genus *Leptodactylus* that occurs in xeric regions of the provinces of Manabí, Guayas, El Oro, and Loja. Yet, towards the central and southern slopes of the Andes in Ecuador, it also occupies moister regions where it is sympatric with: (1) *L. peritoaktites* at Tamarindo in Foothill Evergreen Forest; (2) *L. ventrimaculatus* and *L. melanonotus* at Rio Palenque and surroundings in Lowland Evergreen Forest (Fig. 2).

3　Discussion

3.1　Ecology and natural history of *L. labrosus*

Data presented here suggest that *L. labrosus* is active primarily in the evening, although it can also be active during late afternoon (also observed in *L. ventrimaculatus*, pers. obs.). It is a terrestrial sit-and-wait predator, primarily capturing ground-level and fossorial invertebrates. Earthworms, gastropods, elaterid and scarabaeid beetles, tiger beetle larvae, antlion larvae, terrestrial crickets, and mole crickets are primarily ground-dwelling or fossorial insects (Parmelee, 1999), and account for 24.5% of the diet of *L. labrosus*, even up to 69.4% if ants are included. Flying insects like chrysomelid beetles, dipterans, cicadellids, winged ants, lepidopterans and tettigonid orthopterans are also included in its diet (22.5%). The presence of flying insects might be because of those insects occurring also in terrestrial microhabitats (such as walking on the ground or emerging as winged adults from the litter; Pfeiffer, 1996; pers. obs.) or due to *L. labrosus* sometimes foraging on low vegetation. Stones and soil where present in stomachs with fossorial prey, suggest that frogs possibly eat prey unearthed during fossorial activities. Toxic arthropods like millipedes are unusual preys of leaf litter frogs (Van Sluys et al, 2001), but are reported frequently in various *Leptodactylus* diets (Gallardo, 1958; Parmelee, 1999).

The report of *B. asper* as a predator of *L. labrosus* is published for the first time, but this leptodactylid could be a frequent prey for the pitviper. Both species are present along streams in western Ecuador, and *B. asper* is an active predator of frogs.

Data presented here support the information reported by Heyer & Peters (1971) regarding habitat and microhabitat preferences by *L. labrosus*. In deciduous and semi-deciduous forests, it is found in wet microhabitats around rivers, streams, and drainage ditches. In evergreen forests, its distribution is not restricted by water, as continuous rain and fog maintain more mesic environments and it can disperse farther. *L. labrosus* seems to have higher densities in semi-deciduous than in deciduous and evergreen forests, but monitoring studies are needed to reveal its real abundance and occurrence.

3.2　Distribution of *L. labrosus*

In order to accurately define the distribution of *L. labrosus*, some problematic localities must be clarified.

L. labrosus was described from two female specimens (one still at the Museo Nacional de Ciencias Naturales, Madrid, Heyer & Peters, 1971) given as gifts to Francisco Martinez y Saenz (second zoologist, Comisión Científíca del Pacífico, Savage, 1978) by the naturalist Alcides Destruge (Jimenez, 1875). Both type specimens were cited as being from "Pimocha, orillas del Río Daule" (Jimenez, 1875; Peters, 1955; Heyer & Peters, 1971). According to historical records (e.g. Guayas Historical Archive) and modern maps (IGM, 2000), Pimocha (79°36′W, 01°50′S, 33 m) is located on the margins of the Babahoyo river, and not on the Daule river. Thus *L. labrosus* type locality is: Pimocha, orillas del Río Babahoyo, provincia de Los Rios. Records of *L. labrosus* from Cuzco (Peru) reported by Heyer (1978) were based on two specimens (KU 46443, 46603) from Rio Cosñipata (specimens lost, Heyer & Maxson, 1982a). This population is not included in the distribution analysis of this paper because it is certainly a different species distributed in moist forests of the Atlantic versant of the Andes in southeastern Peru. Heyer & Peters (1971) cited the records of *L. labrosus* by Parker (1938) from the Marañon valley, but they did not re-examine the specimens. Heyer (1978) or Heyer & Maxson (1982a, 1982b) did not report *L. labrosus* from the Cordillera de Huancabamba, and there seemed to be no published references. However, Peruvian researchers mentioned this region in the distribution of *L. labrosus* (Angulo et al, 2004), it is done in this study. Rio Palenque (Scientific/Biological Station) has been cited in the province of Pichincha in the USNM and MCZ catalogs, and in some publications (Larson & de Sá, 1998), but according to the present political divisions of Ecuador, Río Palenque (Scientific Center/Biological Station) is located in the province of Los Rios (00°34′S, 79°20′W, 220 m; Duellman, 1973; Anderson & Jarrín, 2002). Although there are no published records or specimens of *L. labrosus* from the province of Cañar, four specimens (MVZ 77186 – 89) from Cochancay, identified as *L. labrosus* (Museum of Vertebrate Zoology online catalog, incorrectly located on the province of Guayas), and field records from La Troncal (79°20′W, 02°24′S, 460 m; pers. obs.) confirm the presence of *L. labrosus* in the province of Cañar.

The data discussed in this paper along with previous accounts (Vellard, 1956; Heyer & Peters, 1971; Heyer, 1978; Rodríguez et al, 1993; Lehr et al, 2002; Venegas, 2005) indicate that *L. labrosus* is distributed in western coastal Ecuador and northern and central western coastal Peru up to 700 m a.s.l. (highest point Piura, Peru; Venegas, 2005), and into the dry inter-Andean valleys of southern Ecuador and northern Peru up to 1 300 m a.s.l. (Fig. 3). The most northern localities for *L. labrosus* are Playa Escondida and Same, Ecuador (this paper), and the most southern locality is Congón, Peru (Lehr et al, 2002). Its geopolitical distribution in Ecuador includes the following provinces: Esmeraldas, Manabí, Los Rios, Guayas, El Oro, Cañar, Azuay, and Loja, and in Peru the following departments: Tumbes, Piura, Cajamarca, Lambayeque, La Libertad, and Ancash.

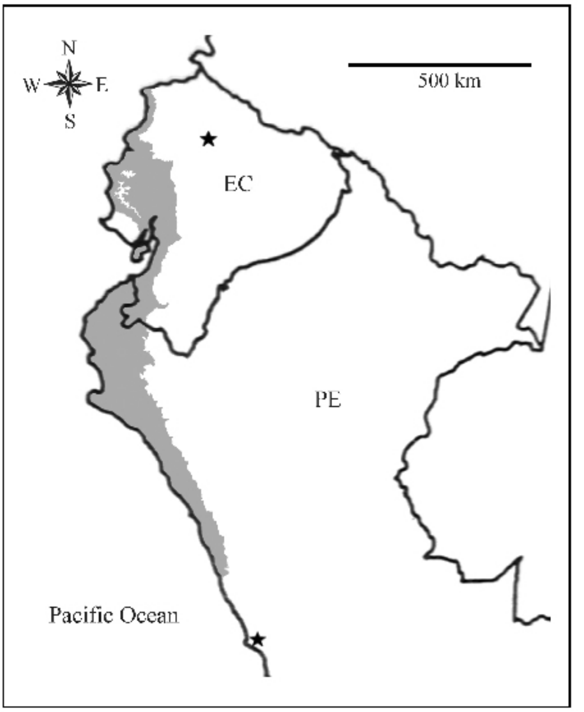

Fig. 3 The projected distribution (shaded area) of *L. labrosus* in Ecuador (EC) and Peru (PE)
Stars indicate the location of the capital cities of Ecuador (Quito) and Peru (Lima).

Along the area of its distribution *L. labrosus* inhabits five vegetation formations: Lowland Semi-deciduous Forest, Lowland Deciduous Forests, Seasonal Lowland Evergreen Forests, Foothill Semi-deciduous Forests, and Foothill Evergreen Forests. *L. labrosus* is mostly restricted to an area called: "Pacific coastal Ecuador and northern Peru seasonally dry forest" (Pennington et al, 2000), "deciduous and semi-deciduous dry tropical forests" (Eva et al, 2002), "dry tropical and dry subtropical regimes" (Lynch & Duellman,

1997), "arid Equatorial region" (Chapman, 1926), "Equatorial dry forest" (Brack, 1986), or "Tumbesian region" (Stattersfield et al, 1998) (Fig. 3). It is the only species of *Leptodactylus* known from these seasonally dry forests along Pacific coastal Ecuador and northern Peru (Heyer & Peters, 1971; Heyer & Maxson, 1982b). The distribution pattern of *L. labrosus* and its sympatry with the other three congeneric species in moister areas (closer to the Choco region or to the Andean slopes) suggest a biogeographic relationship, similar to patterns found in other species of animals from western Ecuador (Anderson & Jarrín, 2002), but different from the forests classification suggested by Sierra (1999), especially for vegetation currently under the name of Lowland and Foothill Evergreen Forests. Anderson & Jarrín (2002) pointed out the existence of two different regions in Lowland and Foothill Evergreen Forests, one being very wet and relatively unseasonal (≤ 4 dry months through the year, Sierra et al, 1999), here called Unseasonal Evergreen Forest, and the other slightly drier and often highly seasonal (usually from June to November), here called Seasonal Evergreen Forest.

Following this new subdivision, *L. ventrimaculatus* is sympatric with *L. labrosus* in Seasonal Evergreen Forest at Rio Palenque, but it completely replaces *L. labrosus* in Unseasonal Evergreen Forest. McDiarmid & Miyata (Heyer & Maxson, 1982a) found habitat segregation between them at Rio Palenque; *L. labrosus* was present in pastures and other parts of cleared or very secondary forests, while *L. ventrimaculatus* was only found in the closed canopied forest (Heyer & Maxson, 1982a). Specimens collected some years ago from the *L. labrosus/ventrimaculatus* contact zone at the surroundings of Rio Palenque were reviewed by Ron Heyer, who noted "there were quite a few specimens that I was unsure which species they were. I wonder if with the amount of deforestation that [L.] *labrosus* is coming into contact with [L.] *ventrimaculatus* much more frequently and perhaps there is some gene exchange going on that wasn't happening before. It would be worth getting a lot of advertisement call recordings and molecular data from a lot of localities of these two species to find out what is going on" (Heyer, pers. comm., 2004). Recent collections from the Río Palenque surroundings found the presence of just two species: *L. labrosus* and *L. melanonotus* (pers. obs., 2004). While *L. labrosus* is adapted to heavily human-altered areas in Seasonal Evergreen Forest (Heyer, pers. comm., 2004; Almendáriz, pers. comm., 2004; this study), *L. melanonotus* is restricted to streams, artificial wetlands, and wet areas near buildings where human gardens and reservoirs provide wetter habitats. *L. ventrimaculatus* seems also able to occupy human-altered areas in Unseasonal Evergreen Forest (even reaching higher relative densities than in closed canopy forest, pers. obs.). It seems to be restricted to closed-canopy situations in Seasonal Evergreen Forest, thus absent or rare at the current deforested surroundings of Rio Palenque, and probably restricted to the 100 hectares of forest protected at the Rio Palenque Scientific Center. This restriction could be related to moisture availability, showing the strong links between environmental/physiological factors and fine-detailed distribution of anurans. Further studies on the dimensional use of space, time and food resources, as well as the relationships of ecological, physiological and environmental variables, are necessary to understand the interspecific interactions between these species at the sites of sympatry (Schoener, 1974; Pianka, 1975; Dure & Kehr, 2004).

A population assignable to *L. ventrimaculatus* was discovered at 550 m on Low Montane Cloud Forest of Cerro La Mocora, a low-elevation montane next to Cerro San Sebastian and part of the Cordillera de la Costa (Fig. 2). It is isolated from other populations of *L. ventrimaculatus* by lowland areas covered by deciduous and semi-deciduous forests where *L. labrosus* occurs (Parker & Carr, 1992). This distribution pattern, where species from the western Andean slopes and evergreen lowland forest are also found in the Cerro San Sebastián-Cerro La Mocora cloud forest, is shared with three species of *Eleutherodactylus*, *Porthidium nasutum* and some species of birds (Parker & Carr, 1992; Lynch & Duellman, 1997; Cisneros-Heredia & Yánez-Muñoz, 2005). At lower elevations of Cerro La Mocora, in semi-deciduous forest, *L. ventrimaculatus* and *L. labrosus* could also be sympatric, but additional collections are needed to determine the existence of a contact zone and its ecological associations.

3.3 Biogeographical Consideration on Western Ecuador

The distribution pattern of *L. labrosus* is shared with various animal and plant taxa: *Artibeus fraterculus* (Mammalia), *Melanopareia elegans* (Aves), *Forpus coelestis* (Aves), *Trachycephalus jordani* (Amphibia), *Dipsas andiana* (Reptilia), *Phyllodactylus reissi* (Rep-

tilia), *Rhodnius ecuadoriensis* (Insecta), *Heliconius peruvianus (Insecta)*, *Cicindella umbrogemmata* (Insecta), and *Pithecellobium excelsum* (Fabaceae) (Jiggins & Davies, 1998; Pearson et al, 1999; Albuja, 1999; Pennington et al, 2000; Abad-Franch et al, 2001). These records (among others) indicate a common pattern of biogeographical history and evolution, and confirm the existence of an important endemic zone that extends through Pacific coastal Ecuador and northern/central Peru in seasonally dry forest, including the southern slopes of the Andes of Ecuador, the northern slopes of the Andes of Peru, and the intervening inter-Andean valleys (Huancabamba, Catamayo). This zone was named the "Tumbesian Region" by Stattersfield et al (1998) in their work on endemic bird areas of the world. Other Ecuadorian anurans apparently restricted (or nearly so) to the Tumbesian Region are: *Bufo amabilis*, *Colostethus elachyhistus*, *C. infraguttatus*, *T. jordani*, *Ceratophrys stolzmanni*, *Eleutherodactylus cajamarcensis*, *Eleutherodactylus lymani*, *Phyllonastes heyeri*, *Engystomops guayaco*, *E. randi*, and *Rana bwana*. Because the Tumbesian region encompasses the overlapping ranges of at least twelve restricted-range amphibian species, I strongly suggest that the Tumbesian region must be considered also an endemic Amphibian area (EAA).

The recognition of the Tumbesian region as a bird endemic area was part of conservation strategies aimed to identify areas with high biological diversity, high endemism, and high conservation priorities (e. g. hotspots, wilderness/endemic/key areas). These strategies resulted from calls by the Convention on Biological Diversity to formulate strategies not only driven by individual countries but with ecosystemic and regional perspectives. They are based on a combination of evolutionary and ecological research and biogeographical analyses (Stattersfield et al, 1998; Myers et al, 2000). Birds are usually the model-organisms for these strategies as they are widely accepted by the public and the knowledge is far more complete and adequate than that of other organisms (Heyer & Vanzolini, 1988; Stattersfield et al, 1998). However, it is generally assumed (principally by non-specialists decision makers) that patterns detected on birds correspond closely to those of other organisms; and the recognition of the Tumbesian region as an endemic area supports this assumption. Yet it is clear that different taxa may show different patterns but the unevenness of data make the evaluation of hypotheses difficult to test these arguments (Heyer & Vanzolini, 1988).

The *Leptodactylus* from western Ecuador show similar distribution pattern to those reported in birds, and in addition to the Tumbesian region, the Chocoan region is the other endemic area recognized in western Ecuador. However, an additional segregation pattern is evident in *Leptodactylus*, mainly by the sympatry of otherwise parapatric taxa at the contact zone between the Chocoan and Tumbesian regions (Fig. 2), and the complete endemicity of *L. peritoaktites* to this contact zone, here referred as having Seasonal Evergreen Forests (Anderson & Jarrín, 2002; this paper). The Seasonal Evergreen Forests has been historically shaped by particular environmental conditions, with influences from climate extremes, mesic (Chocoan) and xeric (Tumbesian) conditions. These abiotic factors have created a particular phyto and zoogeographic zone, in which organisms have evolved on unique ecological scenarios, producing not only particular sympatric patterns but also speciation processes. Among the mammals, three taxa are endemic to the Seasonal Evergreen Forest: *Heteromys teleus*, *Mazama americana fuscata*, and *Cebus albifrons aequatorialis*. *Molossops* (*Cabreramops*) *aequatorianus* could also be endemic to the Seasonal Evergreen Forests (Albuja, 1999). Several birds and amphibians qualify as endemic to these forests: *Chaetocercus berlepschi*, *Pteroglossus erythropygius*, *Colostethus machalilla*, *L. peritoaltites*, *Engystomops coloradorum*, and *E. montubio*. Additional species could also show this endemism pattern but be masquerade under widely-distributed species names (e. g., *E. montubio* was confused with *E. pustulatus* until recently, Ron et al, 2004). Anderson & Jarrín (2002) were the first to recognize this zone as a different zoogeographic unit. I consider that a formal recognition of the area as an independent entity from the Chocoan and Tumbesian regions is important for taxonomic, biogeographic and conservation points of view, and I suggest to call the area: the "West Ecuadorian region" (endemic area), as it is completely restricted to this section of the country (Fig. 2). Additional research is needed to clarify the taxonomic status of several populations of flora and fauna, as certainly more taxa are restricted to the west Ecuadorian region. Unfortunately the west Ecuadorian endemic area is greatly threatened by extreme habitat destruction, and very few forest remnants ensure the long-term persistence of endemic taxa.

Acknowledgements: I am grateful to A. Baquero, M.O. Borja, K. Dammer, D. Mosquera, D. Proaño, T. Sugahara, and J. Tobar for field companionship, laboratory assistance and support; to R. McDiarmid, F. Nogales and D. Almeida for sharing their field data; to A. Almendáriz, A. Bauer, L. Coloma, R. de Sá, W. Duellman R. Heyer, P. Larson, E. Lehr, R. McDiarmid, J. Parmelee, J. Simmons, ECOLAP-USFQ, and the Division of Amphibians and Reptiles, National Museum of Natural History, Smithsonian Institution, for providing literature; To R. Heyer for the identification of *Leptodactylus* specimens deposited at USFQ, and for being willing to discuss special problems. I thank G. Zug, R. McDiarmid and R. Heyer (USNM), A. Almendáriz (EPN), M. Yánez (MECN), and J. M. Touzet and A. M. Velasco (FHGO) for allow examination of material under their care. My deepest gratitude was given to the Smithsonian Women's Committee that allowed me to participate in the 2002 Research Training Program. R. Heyer, R. McDiarmid, K. Swing, M. E. Heredia and an anonymous referee critically read the manuscript. Fundación Natura/Ecuador, Ministerio del Ambiente/Ecuador, C. Zambrano-Machalilla National Park's, M. Negrete, S. Izurieta, R. Sevilla and C. Burneo support different field trips. My gratitude was given to M. E. and L. Heredia for financial and moral support. Universidad San Francisco de Quito provided institutional and in-kind support.

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Appendix 1 Specimens of *Leptodactylus* from the Pacific lowlands and western slopes of the Andes in Ecuador examined for this study. Specimens used for diet analysis are marked with *.

L. labrosus (36): Azuay: Tamarindo (ca. 02°47′S, 79°33′W, 400 m) FHGO 246*, 1206, 1376. El Oro: Arenillas (03°33′S, 80°04′W, 70 m) EPN s/n; Buenaventura (ca. 03°35′S, 79°53′W, 600 m) MYM 2004.378; Machala (03°16′S, 79°58′W, 35 m) DFCH-USFQ 0705*. Esmeraldas: Playa Escondida, 13 km W (by road) from Tonchigüe towards Galera (ca. 00°49′N, 80°00′W, 0 m) DFCH-USFQ 07A; Same (ca. 00°50′N, 79°56′W, 0 m) MECN 2129. Guayas: Naranjal (02°40′S, 79°36′W, 30 m) EPN 4297 – 4301. Loja: Cordillera Mangahurquillo (80°18′W, 04°04′S, 325 m) FHGO 3361 – 63*, 3364; Quebrada de El Faique (04°10′S, 80°02′W, ca. 400 m) FHGO 3396 – 7*, 3398, 3399 – 3402*. Manabí: Agua Blanca, Machalilla National Park (ca. 01°32′S, 80°44′W, 150 m) DFCH-USFQ 10A; Reserva Tito Saltos EPN 8247 – 8258. *L. melanonotus* (4): Esmeraldas: Canandé (ca. 00°25′N, 79°08′W, 450 – 550 m) MYM 2004.679; Concepcion, San Lorenzo (ca. 01°02′N, 78°49′W, ca. 80 m) EPN 5136. Pichincha: Puerto Quito (00°07′S, 79°16′W, ca. 280 m) MECN 2126. Los Rios: town of Rio Lulu, 25 km N Quevedo EPN s/n. *L. peritoaktites* (2): Azuay: Tamarindo (ca. 02°47′S, 79°33′W, 400 m) FHGO 0069, 0248. *L. rhodomerus* (10): Esmeraldas: Canandé (ca. 00°25′N, 79°08′W, 450 – 550 m) MYM 2004.669; Estación Luis Vargas Torres (00°53′N, 78°48′W, 50 m) EPN 8038; San Miguel, canton Eloy Alfaro (ca. 00°45′N, 78°54′W, 180 m) EPN 7862 – 7869. *L. ventrimaculatus* (9): Esmeraldas: Canandé (ca. 00°25′N, 79°08′W, 450 – 550 m) MYM 2004.637, 2004.681; Cerro Mutiles (00°54′N, 79°37′W, 200 – 300 m) EPN 5022. Imbabura: Lita (00°50′N, 78°27′W, 570 m) MECN 2123 – 24, 2130. Manabí: Cerro La Mocora (ca. 01°36′S, 80°42′W, ca. 550 m) DFCH-USFQ 1021. Pichincha: Bosque Protector Mashpi, 18 km N of San Miguel de Los Bancos, on the road between Nanegalito-Pacto-Gualea-Mashpi-Pachijal (00°09′S, 78°50′W, 1 100 m) DFCH-USFQ 0706. Mindo (Hacienda El Carmelo de Mindo) (ca. 00°02′S, 78°46′ W, 1 300 m) DFCH-USFQ 11A-B. San Miguel de Los Bancos, 94 km W (by road) from Quito (ca. 00°01′N, 78°53′W, 1 000 m) DFCH-USFQ 09A-C; San Vicente de Andoas, 9 km E (by road) from P. V. Maldonado or 109 km W (by road) from Quito (ca. 00°05′N, 78°59′, 700 m) DFCH-USFQ 08A-C.